Through a ped darkly: an ecological assessment of root–soil–microbial–faunal interactions

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SUMMARY

1 Studies of ecological interactions in the soil environment require skilled usage of concepts from physics, chemistry, mathematics and biology. This volume offers numerous examples of the multi-disciplinary nature of our work.

2 In each instance—roots as primary producers, root/microbe interactions, interactions of roots, microbes and fauna, and interactions of all three groups with the sand–silt–clay–organic matter milieu (soil)—significant new information has appeared over the last 5 years.

3 Viewing total-system aspects, there have been important findings on resource quality, total-system manipulations, including usage of biocides, in-the-field 'mesocosms', agro-ecosystems, land reclamation and other systems.

4 The added complexity of theoretical aspects of food web design, stability in soil systems, and the short-term physiological and long-term evolutionary implications give us a cornucopia of research topics to study in the next several years.

INTRODUCTION

Overview of the symposium

Our topic, 'Ecological Interactions in the Soil Environment,' is broad and could be more extensively covered in a week than in the two and a half days of the meeting that this volume reports. We will address several major topics in root–soil–microbe–fauna interactions. I shall present some aspects on which we have new information and areas that, if concentrated upon over the next few years, should yield large dividends in information and new insights into soil ecological interactions.

Ecology has been termed 'physiology under the worst possible conditions' (Brock 1966). Interpretation of this remark depends on whether it is observer oriented or soil-organism oriented. Certainly, the organisms living in this opaque gaseous–liquid–solid milieu are growing, if not optimally, then most ingeniously in ways that are only now becoming apparent to us. Perhaps a more venturesome approach to our topic is given by the American poet Wallace Stevens (1954).

> Throw away the lights, the definitions,
> And say of what you see in the dark
> That it is this, or that it is that,
> But do not use the rotted names.
> How should you walk in that space and know
> Nothing of the madness of space,
> Nothing of its jocular procreations?
> Throw the lights away. Nothing must stand
> Between you and the shapes you take
> When the crust of shape has been destroyed.

Let us take the latter course, which, I suggest, using scientific licence, is an invitation to use a holistic, functional approach, i.e. to travel through a ped darkly.

International nature of our work

Work in soil ecology has been truly international in orientation from its inception. I can touch only briefly on these aspects, details of which are well known to many ecologists.

The area of our work on which I would like to concentrate first is the soil itself, its formation, and its development. There have been some true giants in the field, including Lawes and Gilbert in Britain, Berthelot and Pasteur in France, Liebig in Germany, Müller in Denmark, Hilgard and Jenny in America, and Dokuchaev in Russia. A synoptic overview of the field of soil chemistry and biology was presented by Sir E. J. Russell (1923) in a concise and scholarly review entitled 'The development of the idea of a soil population.' He noted the early interest of Georgius Agricola in nitrification four centuries ago, which then, as now, spurred production and industry for warlike pursuits, i.e. production of nitrates for gunpowder.

The history of the controversy between Lawes & Gilbert on the one hand and Liebig on the other is well known. Liebig helped emphasize a dichotomy between organic chemistry (leading to 'humus' formation) and inorganic chemistry, which persists to this day and remains firmly rooted, particularly in North America.

There are a number of historical and psychological reasons for this dichotomy, and we will explore some avenues for removing these barriers. As will become apparent, the interconnected nature of living and dead organic matter above, on, and below the ground surface can best be considered in the context of the spatial milieu in which it exists.

Being primarily biologists, we think of the myriad of biological interactions that occur in the soil system. However, as shown in the detailed diagram of a soil microsite (Fig. 1), there is an immensely variegated array of pores, particles, surfaces, and interfaces. In the last case, entire books have been written about interfaces, and their role in microbial ecology and ecology in general (Marshall 1976; Berkeley *et al.* 1980).

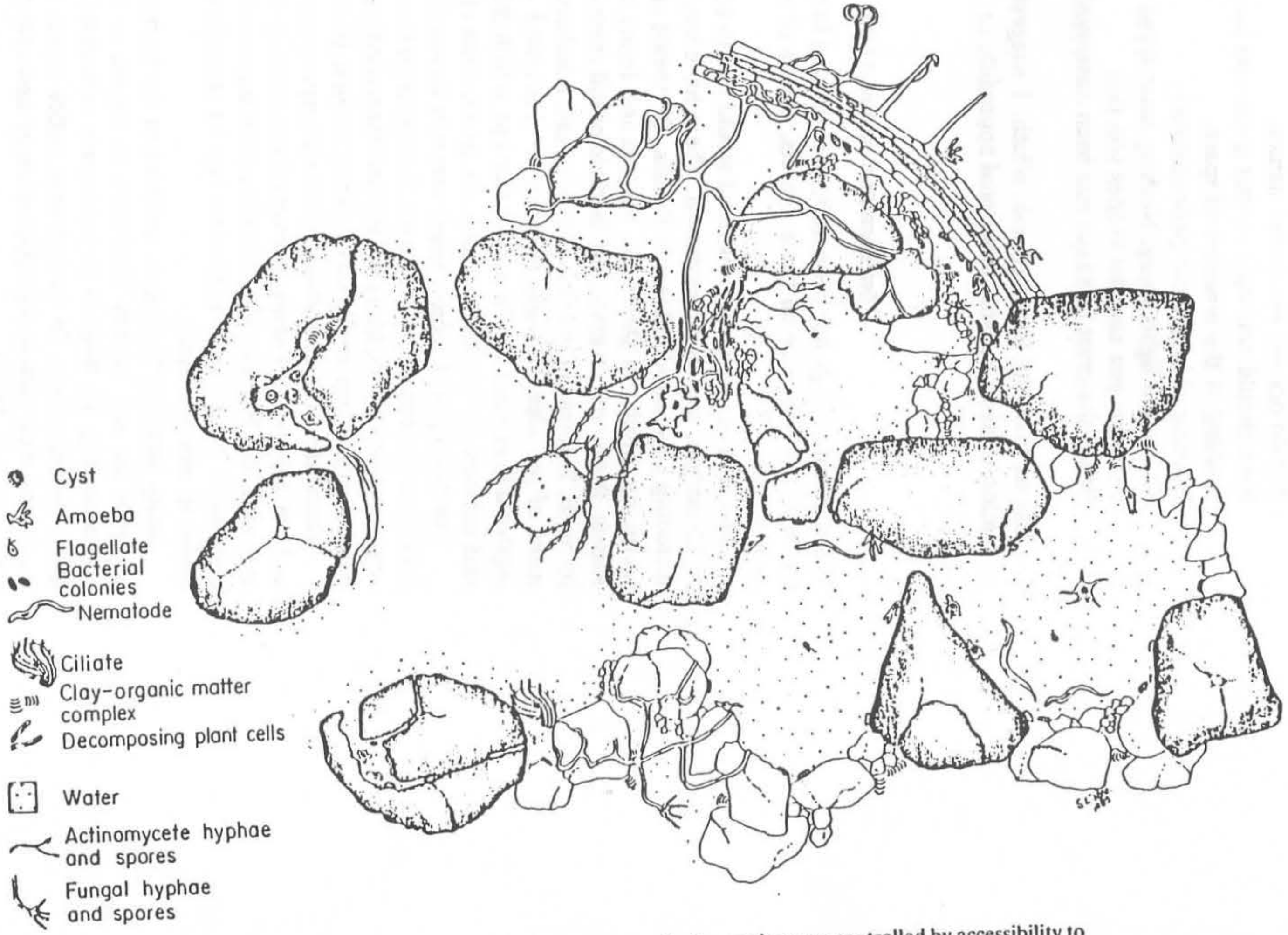

FIG. 1. Trophic relationships among different groups of soil organisms are controlled by accessibility to their resources in this illustration of approximately 1 cm^2 of a highly structured microzone in the surface horizon of a grassland soil (Rose & Elliott, unpubl.).

Soil development: a 'small world'

One of the new themes of the 1980s for ecological work will undoubtedly be miniaturization and integration. Just as many computers have been developed for home and personal use around powerful microchips, we will see more ecological work developing around an integrative approach to, and study of, microaggregates. This work was pioneered by Kubiëna (1938), but has had few adherents until recently. The ways in which particles of sand, silt, and clay are brought together, often via microbial and plant activity (Griffiths 1965; Foster 1981; Tisdall & Oades

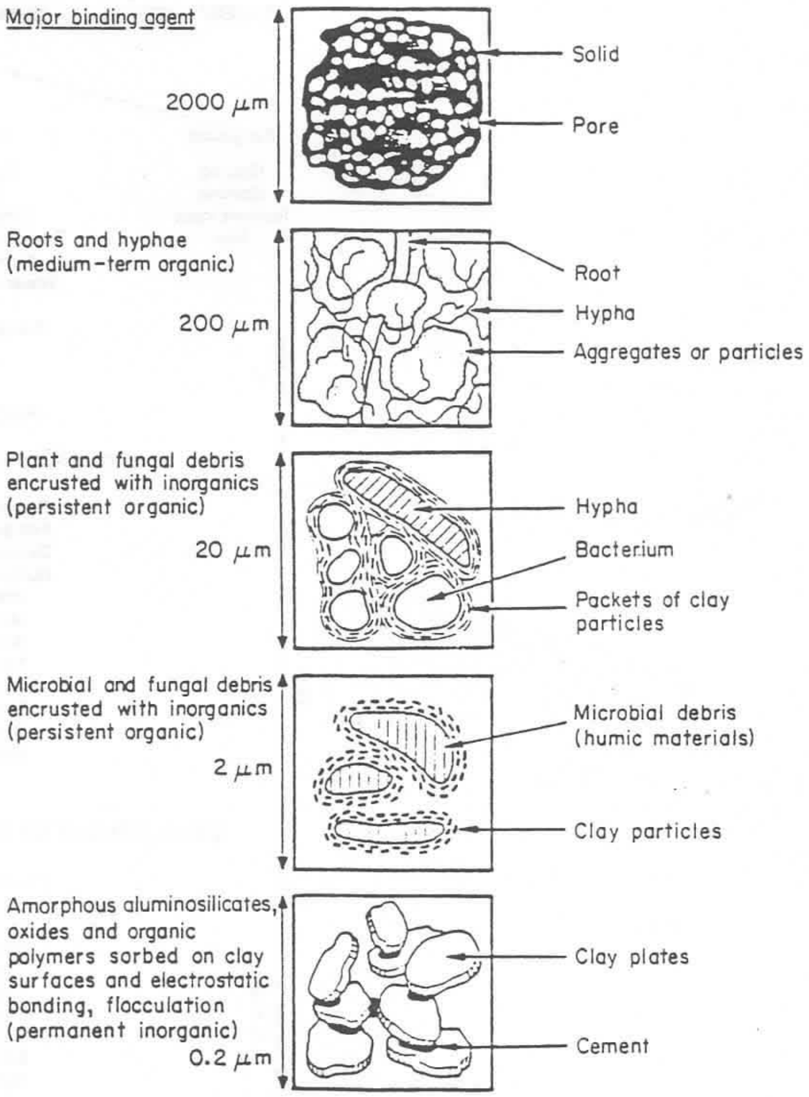
Major binding agent
2000 μm
Solid
Pore
Roots and hyphae (medium-term organic)
200 μm
Root
Hypha
Aggregates or particles
Plant and fungal debris encrusted with inorganics (persistent organic)
20 μm
Hypha
Bacterium
Packets of clay particles
Microbial and fungal debris encrusted with inorganics (persistent organic)
2 μm
Microbial debris (humic materials)
Clay particles
Amorphous aluminosilicates, oxides and organic polymers sorbed on clay surfaces and electrostatic bonding, flocculation (permanent inorganic)
0.2 μm
Clay plates
Cement

FIG. 2. Soil microaggregates, across five orders of magnitude, beginning at the level of clay particles, through plant and fungal debris, up to a 2 mm diameter soil crumb. (From Tisdall & Oades 1982.)

1982) and the ways they affect subsequent organic matter and nutrient dynamics are fascinating. An integrative scheme for levels of aggregation from a fine clay particle up to a 2 mm microaggregate is shown in Fig. 2. A series of these form a macroaggregate, or crumb. In a native, undisturbed soil, the arrangement of crumbs ~~in an aggregate~~ is called a *ped*, which is a diagnostic soil structure, reflecting the parent material and the various factors that affected the soil formation process.

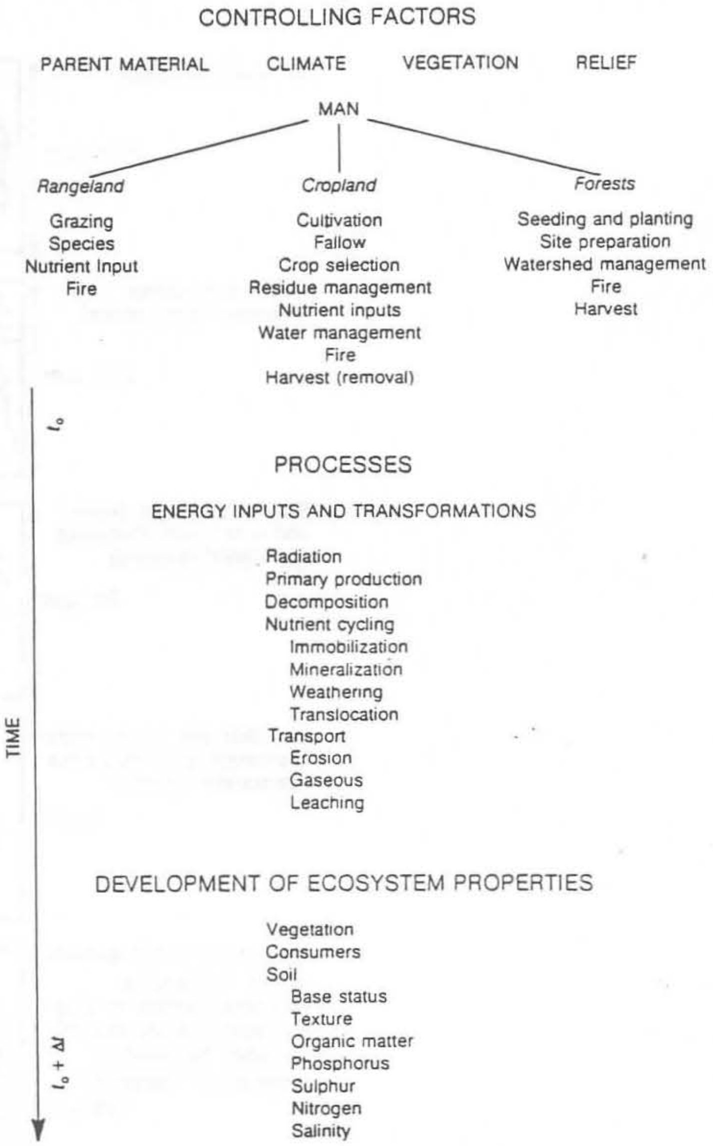

FIG. 3. Soil-forming factors, and major processes, over time, lead to development of ecosystems properties. (From Coleman *et al.* 1983.)

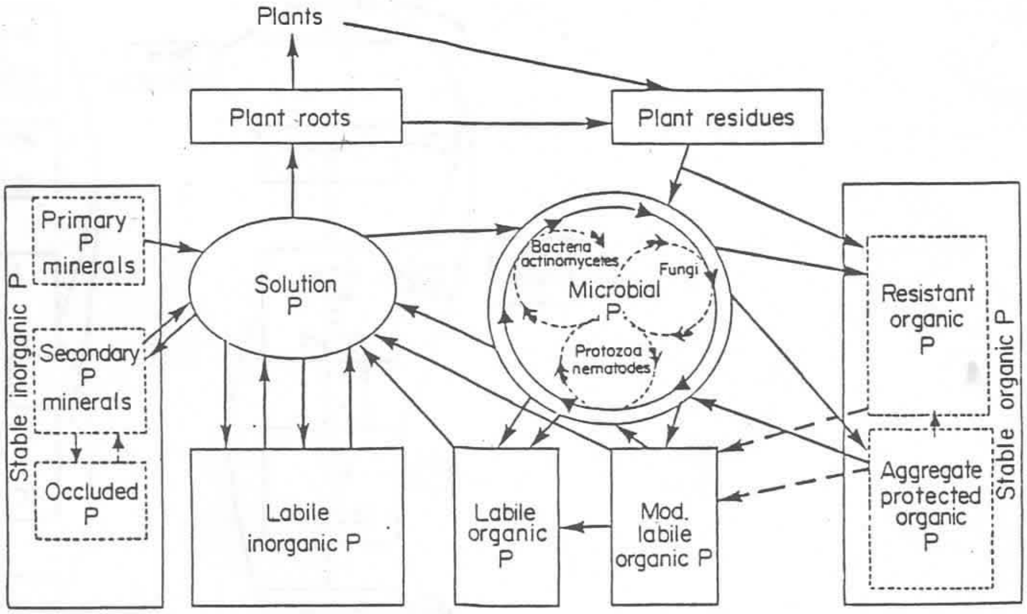

FIG. 4. Flows of inorganic and organic forms of phosphorus. Microbial and faunal interactions affect flows of labile inorganic and organic P. (From Stewart & McKercher 1982.)

Jenny (1941) succinctly described an equation for soil formation:

$$\text{soil formation} = f(cl, o, p, r, t),$$

where cl = climate, o = organism, p = parent material, r = relief, and t = time. It may be of greater use if we envisage soil-forming factors, with several key processes, including immobilization, mineralization, leaching, etc., which lead over time ($t + \Delta t$) to soil properties (Fig. 3; Coleman, Reid, & Cole 1983). This viewpoint was first noted, in a different form, by Stephens (1947); cited by Burges (1960).

Soil-forming processes occur over thousands of years in chronosequences. They have been characterized by Crocker & Dickson (1957) and Dickson & Crocker (1953) for nitrogen dynamics and Walker (1965) for phosphorus. Because P is a fundamental limiting nutrient in both aquatic (Hutchinson 1957) and terrestrial (Cole & Heil 1981) milieux, the availability of labile inorganic forms of this element (as phosphate ions) may be crucial for subsequent inputs and fluxes of nitrogen and carbon in the ecosystem. Some of the biotic and chemical transformations are summarized (Fig. 4) by Stewart & McKercher (1982). As I shall emphasize repeatedly, the turnover rate of a relatively small pool (i.e. labile inorganic) is far more important than pool size. For example, the larger but less dynamic non-labile inorganic and organic pools may contribute only a small fraction to annual nutrient fluxes, compared with the small highly labile pool.

One of the major findings of groups in our laboratory and elsewhere in North America and Europe has been the central role microbial production and turnover plays in these processes. This interplay between microbes as primary decomposers and organic matter as a substrate to be decomposed has been incorporated in a

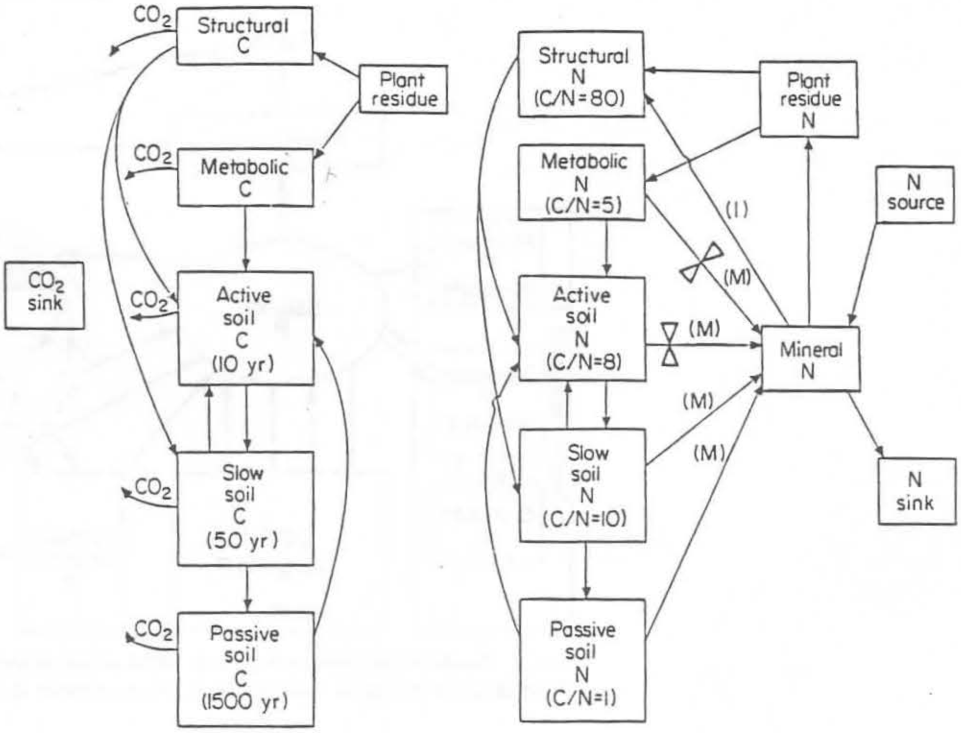

FIG. 5. Flows of structural, metabolic, and soil N and C in a soil organic matter model. Note faunal–microbial interactions, represented by ⧗ from 'metabolic' and 'active' N boxes. 'I' = immobilization and 'M' = mineralization processes. (Modified from Parton *et al.* 1984.)

mathematical simulation model for an agro-ecosystem by Parton *et al.* (1984). The model (Fig. 5), developed to simulate organic matter dynamics over decades and centuries, does not explicitly separate bacteria and fungi or include activities of grazing fauna. However, by accounting for inputs of organic matter of various quality (e.g. C:N ratio, fraction that is labile), the model adequately mimics observed changes in organic matter content on continuously cropped versus alternate wheat–fallow rotations in dryland wheat fields of the northern Great Plains. Interestingly, another version of the model, developed in conjunction with J. Persson and colleagues in the Swedish arable lands project, accurately reflects changes in organic matter inputs in regularly burned fields versus fields that have stubble incorporated into them.

MAJOR TOPICS TO BE COVERED

Our topics run the gamut of subjects concerning the soil environment: the root as primary producer; interactions with soil microbes; effects of grazing animals; interactions in soil and ecosystem function. These constitute some twenty papers plus posters on the same topics. Rather than attempt to give a synopsis of each presentation, I will make a few comments on each topic, discuss some new developments, and then attempt a synthesis of concepts and information.

The root as primary producer

Drs Fogel, Atkinson and Fitter present information on roots as substrates but also 'outposts', as it were, in the continuous struggle required for nutrient uptake by plants and growth and maintenance.

Roots are amazingly labile and highly varied in their growth and reactions to environmental stimuli, both abiotic and biotic. A complex array of techniques has been developed for determining distribution and activity of functional (metabolically active) roots (Singh & Coleman 1977), which has been summarized by Böhm (1979).

The amount of detailed information required for population, community, or ecosystem level research will vary but, as noted by all three speakers, we must have better measurement of changes in root production and intra-season and annual turnover. The crude practice of sequential harvesting of fibrous roots may give erroneous estimates of below-ground production. Biomass estimates depend heavily on identification of maxima and minima in standing crops of roots. If these are the result of sampling bias, rather than real trends, either overestimates or underestimates of true production will result (Singh *et al.* 1984). With from 30 to 50% or more of high-quality material coming from rhizodeposition (Shamoot, McDonald & Bartholomew 1968; Sauerbeck & Johnen 1976; other references in Fogel, p. 23), we obviously require suitable integrative techniques to measure these inputs; isotopic tracers, including stable isotopes, and other functional measurements will be useful tools for many of us.

Interactions with soil microbes

Here we arrive at the crux of several issues before us as soil ecologists. Whether dealing with rhizosphere, soil, or litter; inputs or outputs; co-operative or disoperative (Allee *et al.* 1949) interactions, surely a careful study of rhizosphere phenomena (Newman; p. 107; Giller & Day, p. 127), litter decomposition (Paustian, p. 159), mycorrhizas and nutrient cycling (Read, Francis & Finley, p. 193), and root-microbial (including protozoa) associations (Clarholm, p. 355) will be informative areas of ecosystem functional studies.

One of the major challenges in soil ecology, as in all science, is to keep an observant eye out for important patterns, processes, and their implications. Some examples of these are: (i) if annual and perennial plant rhizospheres are fundamentally different, what does this mean for the ways in which we study root-microbial interactions? (ii) Does the root–microbe–fauna complex significantly affect symbiotic and nonsymbiotic N_2 fixation? (iii) Do the intra- and interspecific bridges between plants via mycorrhizas (Chiariello, Hickman & Mooney 1982; Read, Francis & Finlay, p. 193) form an important mechanism for both N (Ames *et al.* 1983) and P uptake, and does this extend to water uptake and other often limiting factors as well?

The effects of root–microbe interactions on organic matter transformations are an increasing area of inquiry. Both in terms of negative effects of roots on aggregating properties of native soil polysaccharides (Reid & Goss 1981, 1982a) and as net inhibitors of mineralization of labile ^{14}C organic matter (Sparling, Cheshire & Mundie 1982; Reid & Goss 1982b, 1983), it seems apparent that simple heterotrophic soil incubations are missing some important interactions provided by a growing root system.

Effects of grazing animals

Studies of mesofauna and macrofauna and their effects on other biota, including bacteria, fungi, roots, and root–mycorrhizal associations continue as a burgeoning area of research (Anderson, Ineson & Huish 1983; Seastedt 1984). Several years ago, my colleagues and I espoused a somewhat simplistic approach to microbial–faunal interactions (Coleman 1976), emphasizing the positive, system-level benefits of enhanced nutrient return (Coleman *et al.* 1977). With the benefit of hindsight, I shall emphasize the multifarious nature of these interactions. In studying plant–animal and animal–microbial interactions, we should know the physiological state of the grazer and grazed populations. Thus, under certain conditions, with actively growing tissues, a low to moderate amount of grazing (Fig. 6) may enhance plant or microbial growth (Dyer & Bokhari 1976; Dyer *et al.* 1982; Hunt *et al.* 1977). Fungal growth response to collembolan grazing is closely dependent on the nutritional state (nutrient content) of the fungal hyphae being grazed. Do fungus-grazing animals preferentially feed on the young, actively growing parts of hyphae? Recent work by Ingham *et al.* (1985) in our laboratory indicates that fungal-feeding nematodes consume amounts of fungal cytoplasm greater than the amounts that stain with FDA (Söderström 1977).

Perhaps more important for field-related phenomena, what is the importance of the repeatedly demonstrated preference of certain fungal-feeding fauna for particular species of fungi (Coleman & Macfadyen 1966; Parkinson, Visser & Whittaker

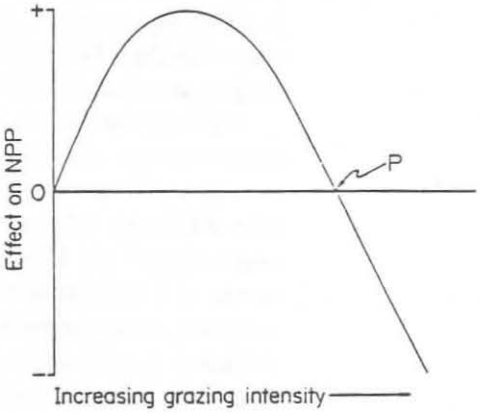

FIG. 6. Optimization of production as a function of grazing. Note peak at low → moderate grazing rates. (From Dyer *et al.* 1982).

1979; Newell 1984) or bacteria (Führer 1961) in subsequent ecosystem function? Do these interactions extend more generally to 'disease suppressive' soils (Schroth & Hancock 1981)? Recent work from Australia shows some intriguing amoebal–pathogenic fungi interactions which bear further study (Chakraborty, Old & Warcup 1983; Chakraborty & Warcup 1983). Recent reviews of microarthropod feeding relationships are given by Petersen & Luxton (1982) and Cancela da Fonseca & Poinsot-Balaguer (1983), and by Visser (p. 297).

An additional topic of great interest is mycorrhiza–fauna interactions. Extensive research in crop plants (e.g. *Gossypium*, *Citrus*) has shown little, if any, effect of fungal-feeding nematodes on subsequent plant growth (Hussey & Roncadori 1981, 1982)). Therefore, it will be interesting to see if microarthropod feeding on VAM external hyphae is generally deleterious or not; an approach to this is discussed by Finlay (p. 319).

Other aspects of plant–animal–microbial interactions will be addressed in the next section, on soil and ecosystem function.

Interactions in soil and ecosystem function

An extensive and intriguing set of topics are presented within the general rubric of soil interactions and ecosystem function. We need to be as percipient and integrative as possible. One approach that may be of considerable utility now and in the future is the 'unit community' concept of Swift (1976). He noted that many organisms in the decomposer community play similar roles and that dynamics of various cellulolytic or ligninolytic microflora may differ between neighbouring branches or logs in a forest floor, but the overall processes and rates at which they proceed will be largely independent of the species composition in the substrate itself. This is paralleled by earlier observations of Fager (1968), who showed the stochastic nature of meso- and macrofaunal colonization and exploitation of experimental oak logs in Wytham Wood.

The problem of resource quality and how best to quantify it arises in several papers in our meeting. A holistic approach should include study of the mineral, as well as the biotic, components. The work of Kilbertus & Vannier (1981), and Touchot, Kilbertus & Vannier (1983) is exemplary in this regard. They observed that eu-edaphic species of *Tomocerus* or, in laboratory conditions, *Folsomia candida* tended to ingest small amounts of argillic (clay) material, which helped detoxify various phenolic compounds in oak (*Quercus*) leaves. Even more interesting, bacterial development in the aggregates formed was promoted during gut passage. Thus, the bacterial colonies were included in a mucus layer surrounded, in turn, by a layer of clay minerals.

The long-term effect of these processes on faecal-material decomposition requires further study. Jongerius (1964), Zachariae (1965), Rusek (1975), Kühnelt (1976), and others have commented on the nature, extent, and persistence (over several years) of faecal pellets of microarthropods in a wide variety of ecosystems.

SYSTEM-LEVEL MANIPULATION OF SOIL ORGANISMS

In recent years, there has been a renewed interest in manipulation of system components in soils. This developed from some of the uses of atomic energy in ecology and was summarized in various publications sponsored by the US Atomic Energy Commission (e.g. Odum & Pigeon 1970). More specific studies of manipulation of soil arthropods were noted by Edwards (1967) and soil biota in general by Coleman & Cowley (1973). The latter study showed marked changes in soil respiration; but, as one might expect, only when primary decomposers (bacteria and fungi) were drastically reduced or totally removed by several Megarad (10^4Gray)-level doses of gamma radiation. Use of high-energy gamma-emitting sources is restricted in its utility worldwide, and other, more general approaches were desired.

In our studies at CSU, we decided on a 'bottom-up' approach, assembling oligo-specific groups of microflora and fauna, with and without seedlings growing in them, in gnotobiotic microcosms. Our main conclusions have been reported in Coleman *et al.* (1983, 1984) and are discussed only briefly here.

In either heterotrophic microcosms or with heterotrophs and autotrophs combined, we observed significant mineralization of organic N and P (Fig. 7), or nitrogen alone (Fig. 8). Because of inherently greater net mineralization potential by saprophytic fungi than bacteria in some of our experiments, the holophagic nature of the protozoa or bacterial-feeding nematodes seems to have a greater impact on the nutrient return than the fungus/fungivore association (Ingham *et al.* 1985).

It became apparent that, to approach a true system-level species richness more readily, we would need to begin studies using a 'top-down' approach, with selective elimination of target groups of organisms. The rationale for this approach, i.e. using 'perturbation experiments', has been ably summarized by Usher, Booth & Sparkes

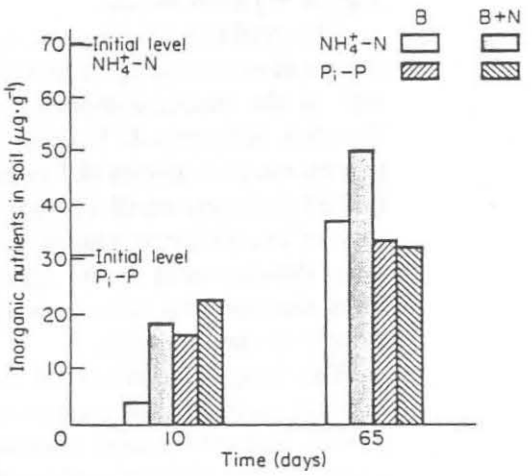

FIG. 7. Mineralization of inorganic N and P in soil microcosms with (B + N), and without (B) bacterial-feeding nematodes. Significant differences ($P < 0.05$) were observed for N and P on day 10. (From Anderson *et al.* 1981).

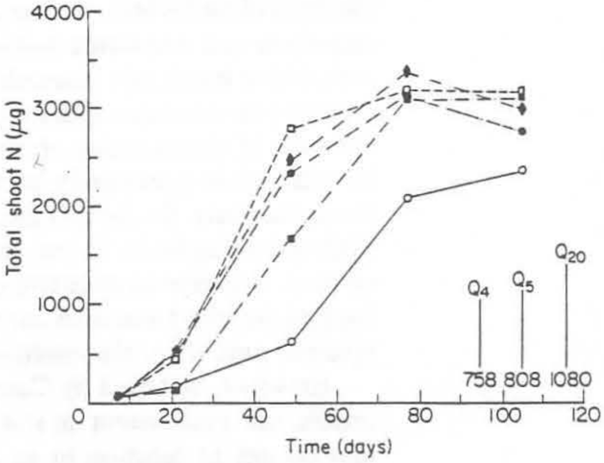

FIG. 8. Mineralization of N, and facilitated uptake, in the presence of bacterial or fungal grazers (----) versus plant alone (——). (From Ingham *et al.* 1985).

(1982), and assessed for real and idealized communities by Bender, Case & Gilpin (1984), who observed various responses, depending on pulsatile ('pulse') versus continued ('press') types of perturbations. One of the major difficulties of performing whole-system perturbation experiments is adequately to distinguish between direct and indirect effects of organism removal.

Drawing on some earlier concepts reported before a British Ecological Society audience (Coleman 1976), we tried manipulating soil 'functional groups' (e.g. bacterial-feeders, fungal-feeders, etc.) where possible. We devised a major field experiment, using six biocides specific for the following groups: bacteria, saprophytic fungi, phycomycetous fungi (including vesicular-arbuscular mycorrhizae), nematodes, acari, and all arthropods. This study ran for 6 months and generated large amounts of interesting but as yet unpublished data.

Unfortunately, most of the available biocides are specific for most or all organisms in a major taxonomic group, such as arthropods or nematodes. These transcend, of course, the desired functional constructs, e.g. bacteriophages, fungiphages. Therefore, we have proceeded with an alternative approach, namely, a mathematical simulation model. We set up a conceptual model of nitrogen flow consisting of shoots, roots, two categories of substrates, and some eleven groups of fauna that feed directly or indirectly on bacteria (including actinomycetes), fungi (including VAM), or other fauna.

In developing this model, we were impressed by two things: the many interconnections occurring, particularly at the higher trophic levels, and the long chain length of some of the pathways. For example, going from substrate to microflora to amoebae, via intermediate predators, to predatory mites entails going through seven trophic levels. This is longer than any food chains studied in the classic paper of F. E. Smith (1969) or the recent book of Pimm (1982).

As noted by May (1973a,b) and Pimm (1982), these systems, containing a plethora of omnivores, should be inherently unstable, both in terms of populational responses and associated nutrient-cycling responses (DeAngelis 1980). This is an area where much new research is currently being conducted in theoretical ecology. Drawing on extensive data summarized by Briand (1983), Yodzis (1984) addressed the issue of commonness or rarity of omnivory. He concluded that omnivory tends to occur more prevalently between organisms in similar trophic positions than in those far apart. So far as I can ascertain, there was no input of information from litter-soil ecosystems in the array of forty data sets, from terrestrial and aquatic systems. We have an excellent opportunity to assess whether omnivory, particularly feeding on prey more than one trophic step away, is unusually common in litter-soil systems, and, if so, the implications for ecosystem resilience.

However, as noted by Coleman *et al.* (1983), Yeates & Coleman (1982), and others, the 'real system' in soil is truly resilient, contains many cryptobiotic forms, and refuses to function in as simplistic a manner as we have so far managed to portray it. The main problem is how to represent considerable detail, yet keep the model to manageable proportions. It is apparent that we must adequately represent the extent to which much of the soil biota enter into, and exit from, quiescent, dormant, or cryptobiotic stages (Demeure *et al.* 1979; Stout *et al.* 1982).

Some initial simulation runs of the biocide model (Fig. 9) showed that predatory forms of soil arthropods and nematodes were very sensitive to changes in abundance of the bacterial or fungal populations (H. W. Hunt *et al.*, unpublished data).

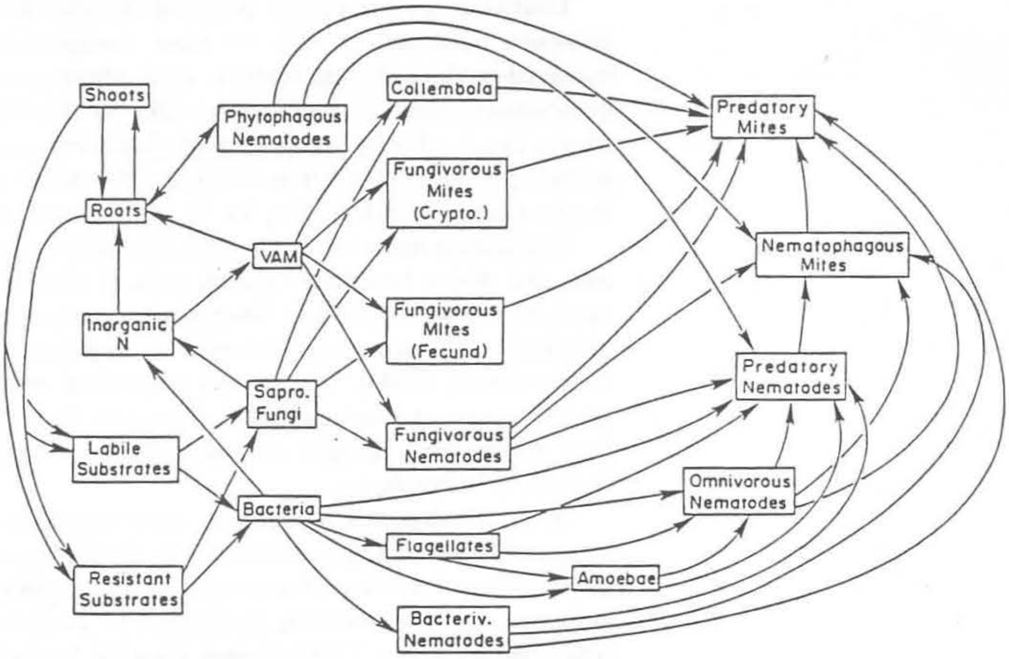

FIG. 9. A model of trophic interactions among plants, substrates, microflora, and fauna in a shortgrass prairie. (From Hunt *et al.* unpubl.)

New research in the next decade

One of our major concerns should be how best to cope with various levels of resolution in the soil–root–biota system. It is fruitful to review what others have said about the 'cardinal entities', as it were, in ecology. Watt (1968) claimed that all of ecology considers matter, energy, space, time, and diversity. Having dealt with all of these to an extent, I would like to pursue some further ideas on time and size. In an address to this society, Burges (1960) discussed with great insight the manners in which time and size affect ecological processes, both successional and longer-term, including soil formation and the chronosequences which I mentioned briefly earlier.

I shall address some aspects of size. Burges expressed concerns about methods to sample communities which are small in relation to ourselves, concerns which were further amplified by Macfadyen (1969). Organisms within the community play markedly different roles as a function of size. Thus, organisms (microbes, protozoa, small nematodes, rotifers) which exist in water films, in various micropores within soil, are probably operating in a quite different 'world' from the organisms which move into and out of pores, independently of water films. A third, and perhaps even more distinctive category are those members of the macrofauna which move soil around by external means (fossorial mammals) or internal means (earthworms) (Hole 1981).

Of course, Charles Darwin (1837, 1881) played a pioneering role in investigating activities of earthworms. Numerous other books and papers refer to earthworms' function in soil, summarized by Edwards & Lofty (1978), Bouché (1983) and Lavelle, Zaidi & Schaefer (1983). Recent work in New Zealand (Sharpley *et al.* 1979; Syers *et al.* 1979) gives further indication of how these organisms affect nitrogen and phosphorus dynamics in pastures. The paper by Springett (p. 399)

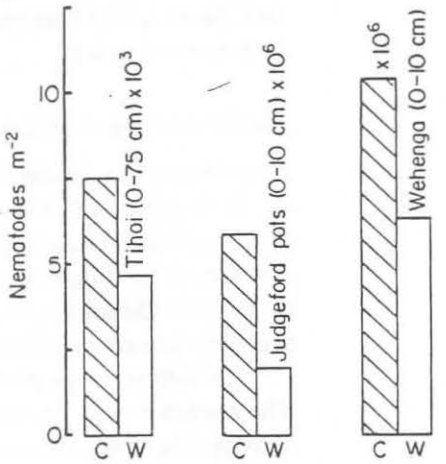

FIG. 10. Nematodes per m^2 in field sites in New Zealand (Tihoi, Wehenga) or in pot trials (Judgeford) with (W) or without (C) earthworms present. (From Yeates 1981).

develops some themes in this area, such as impacts on root growth. My comments are meant to be complementary to hers.

In addition to having an effect on plant debris through trituration and comminution, earthworms in New Zealand were found markedly to depress soil nematode populations in both laboratory (pot experiments) and field sites. Nematode standing crops were only 40–50% of those in treatments (Fig. 10) which had no earthworms (Yeates 1981). Similar decreases, in laboratory studies, have been observed after earthworms' ingestion of protozoa (Piearce & Phillips 1980). We have no information yet on effects on population growth rates of these 'prey' populations but, with our concern for measurement of turnover rates mentioned earlier, this is an important factor to consider in future ecological field studies.

Perhaps geophagy should be more generally considered with other members of the soil fauna. I assume that a certain amount of soil is ingested by millipedes and isopods. The structural and biochemical impacts (e.g. P mineralization) of the little-studied soil-eating termites has also been noted (Wood *et al.* 1983).

A further aspect of ecosystem function is the time at which activity occurs. Dr Verhoef discusses interesting aspects of collembolan activity in pine forests in mid-winter (p. 367). The cumulative effect of soil organisms living at or near 0°C, whether cryophilic or not, is an important area for further work in ecosystem function.

Distributions of organisms, relative to organic matter in soil

One of the interesting findings to emerge from our soil ecology studies over the last few years has been the commonality of patterns of distribution and abundance of soil organisms. Both roots and VA mycorrhizal hyphae proliferate locally when they reach a zone of organic matter enrichment (St John, Coleman & Reid, 1983a,b). The implications of proliferation of many types of organisms, such as roots, mycorrhizal fungi, microbes, or fauna with associated organic matter may well be an area of interest which will continue to develop in soil ecology over the next several years.

Studies in agro-ecosystems

Another aspect, in the basic/applied ecology realm should be considered by all of us. It is apparent that, with greatly increasing amounts of land area going into minimum- or zero-tillage, we should be alert to developments and opportunities in this area. The following is some recent information from studies we have conducted in Eastern Colorado, in dry-land wheat (Elliott *et al.* 1984a,b). The results discussed here are from a fallow, no-till treatment in a silt-loam soil (Argiustoll).

The site was sampled over five times in summer 1982 (5 June–13 September). The season was quite moist, with adequate water available for microbial and faunal activity the entire summer. We observed marked dynamics in faunal activity throughout the summer. Acari were greatest in early June, and continued to decrease through to September (Fig. 11). Holophagous nematodes (principally

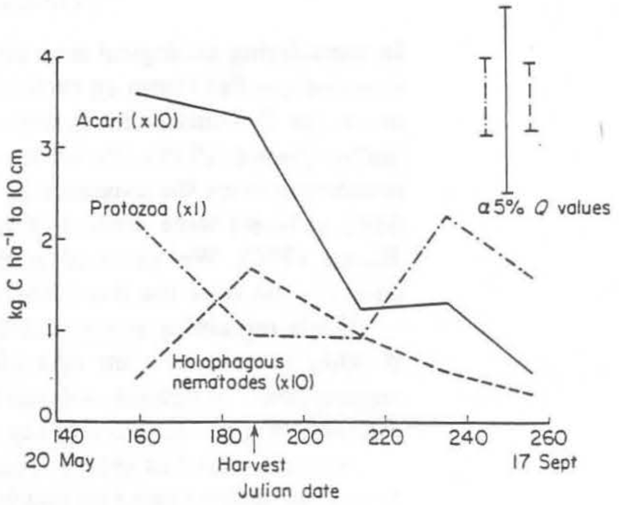

FIG. 11. Soil faunal dynamics in the fallow side of no-till plots at Akron, Colorado (1982). Note early tenfold greater biomass of protozoa, mostly amoebae and flagellates. Means between dates farther apart than confidence intervals are significantly different at $P < 0.05$. (From Elliott *et al.* 1984).

bacterial feeders) reached a peak in early July, while protozoa had early and late summer peaks of biomass. Microbial C and P were low in early and late summer, corresponding with peaks of protozoan biomass (Fig. 12). We suggest that these results correspond well with the classical results of Cutler *et al.* (1922), and the microcosm studies of Coleman *et al.* (1978) and Cole *et al.* (1978). Perhaps these interactions can be considered along with the aspects of phytotoxicity, nitrogen fixation, etc., covered by Lynch in this symposium (p. 181).

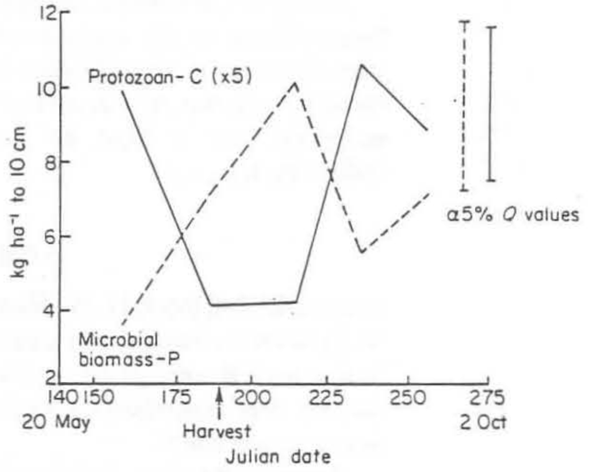

FIG. 12. Dynamics of microbial biomass P and protozoan C in fallow no-till and stubble-mulch plots, Akron, Colorado, showing inverse relationship. Sample dates are the same as in Fig. 11. Confidence intervals calculated as in Fig. 11 (From Elliott *et al.* 1984b).

CONCLUDING REMARKS

In considering ecological interactions in the soil as a whole, we would do well to examine our field from an evolutionary perspective. From the time that a land flora arose (in Devonian times), there were numerous phycomycetes associated with plants (Swain 1978). However, more interestingly, it may have been a virtual precondition for the existence of Tracheophytes that mycorrhizas (phycomycetous ones, at least) were present (Pirozynski & Malloch 1975; Malloch, Pirozynski & Raven 1980). We know of many ideas on insect–angiosperm development and co-evolution over the last 150–200 million years.

While remaining appropriately cautious about advancing these ideas, I wonder if other symbiotic, even mutualistic, associations arose once gymnosperms and angiosperms appeared on earth, in addition to the obvious examples of *Rhizobium* spp. and *Frankia* spp. symbioses?

Anyone who has seen a 'rhizotron' time-lapse cinematography film (the one from East Malling being among the more noteworthy) cannot help but wonder about the sequence at a growing root tip: sloughed root cap cells, exudates, exfoliates, in turn driving microbial activity, and subsequent faunal feeding and mineralization. There may be some important mutualistic relationships there, waiting to be studied.

There has been a resurgence of interest in mutualistic relationships in biology, and opportunities for group selection (Boucher, James & Keeler 1982). While not wishing to rekindle the fiery controversy ignited by Wynne-Edwards (1962), the concepts of Wilson (1980), who showed weak selection pressures for mutualistic associations, are both plausible, and amenable to new research using more holistic, ecosystem-oriented approaches. Even though this conference is being held in the home country of William of Ockham, perhaps we would do well to put as least as much effort into a synthetic, 'anabiotic' (Lotka 1925) approach to ecology, as we often put into the more fashionable, reductionist approach.

Many of the holistic, multidisciplinary studies which are required in soil ecology bear witness to the remarks of Sir E. John Russell (1923) who said: 'The soil population is so complex that it manifestly cannot be dealt with as a whole in any detail by any one person, and at the same time it plays so important a part in the soil economy that it must be seriously studied. Team work therefore becomes indispensable . . .'

ACKNOWLEDGMENTS

I thank E. T. Elliott, H. W. Hunt, E. R. Ingham, R. E. Ingham, J. C. Moore, and T. V. St John for helpful comments on the manuscript. Several of the ideas presented in this review were developed and/or encouraged to fruition by Professor A. Macfadyen. His contributions to the field of soil ecology are truly noteworthy, and much appreciated.

Support for ideas developed in this paper was provided by grants from the US National Science Foundation. Support from the BES to attend the meeting and present this paper is gratefully acknowledged.

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